Relaxed selection when you least expect it: why declining bird populations might fail to respond to phenological mismatches

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Relaxed selection when you least expect it: why declining bird populations might fail to respond to phenological mismatches

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Ongoing climate change threatens to cause mismatches between the phenology of many organisms and their resources. Populations of migratory birds may need to undergo 'evolutionary rescue' if resource availability moves to earlier dates in the year, as shifted arrival dates at the breeding grounds may be required for persistence under new environmental schedules. Here we show a counterintuitive process that can reduce the strength of selection for early arrival when the resource peaks earlier. This happens when two processes combine to determine selection for early arrival: breeding success is higher if a bird does not miss the resource peak, but this occurs together with a 'zero-sum game' where birds acquire good territories ahead of their competitors if they arrive early. The latter process can relax if the population has experienced a recent decline. Therefore, climate change can have two opposing effects: its direct effect on breeding success strengthens selection for early arrival, but this combines with an indirect effect of relaxed selection due to population declines, if territoriality is a significant determinant of population dynamics and fitness. We show that the latter process can predominate, and this can cause a failure for a population to adapt to a new schedule under changing environmental conditions.

Recent climate change, resulting in rapid global warming (IPCC 2007), threatens to cause mismatches between environmental (often climatic) cues and triggers of life history schedules (Visser and Both 2005). Such mismatches can have significant negative population consequences (Both et al. 2006). Rapid climate change has therefore the potential to severely impact a large number of species, as a failure to adapt to changed seasonal cues can lead to population declines and potentially extinction. To the extent that such adaptation is genetic, it can be considered a form of evolutionary rescue: a mismatch can be considered a form of 'stress' that leads to population decline unless selection produces a new gene pool that is capable of establishing positive growth rates in the new environment (Bell 2013).

Of particular interest is avian spring migration. Over the past decade, spring has advanced in temperate regions of both the northern (Schwartz et al. 2006) and southern hemispheres (Chambers et al. 2013), shifting abiotic conditions and resource availability to earlier dates in the year (though not necessarily uniformly across the hemispheres nor over smaller spatial scales). Therefore, the optimal time of reproduction for migrating birds has also shifted: arriving too late imposes a penalty if the feeding of young can no longer coincide with the peak of resource availability (Drent et al. 2003, Jonzén et al. 2007). Although there is plenty of evidence of birds now arriving earlier than in previous decades (Root et al. 2003), the arrival time of birds has not always shifted as much as the resource availability (Both 2010). Long-range migrants in particular are not adjusting enough to compensate for the speed of climate change, resulting in increased ecological mismatch and accumulation of a 'thermal delay' (Saino et al. 2011). As this can lead to severe population declines (Both et al. 2006), it is important to understand why populations do not necessarily keep pace with environmental change.

There are several suggested reasons for mismatched timing, as birds do not advance their arrival and breeding at the same rate as the environment shifts. Climate change may not cause all components of the phenology of a migrating bird to shift at the same rate (Visser et al. 2004). Arrival date changes to track resource advancements at the breeding grounds might thus only occur if circumstances change similarly along the entire journey (Both 2010). It may be more difficult to adjust to seasonal cues if they have to be observed over large spatiotemporal regions, yet long-distance migrants do not appear to be less able to respond (Jonzén et al. 2006) than short-distance migrants. The cues used may also be unrelated to climate (e.g. photoperiod, Coppack and Both 2002), in which case changed schedules are not expected unless there is a microevolutionary response such as migration at a different photoperiod length than before. Intergenerational parental effects, where early laid eggs hatch birds that themselves migrate early as adults, are also possible (Gill et al. 2013).

Johansson and Jonzén (2012a, b) have also pointed out that it may be incorrect to assume that the mismatch was historically nonexistent. Game-theoretical treatments of competition for territories (Kokko 1999, Jonzén et al. 2007,

Johansson and Jonzén 2012a, b) show that populations of territorial species are expected to arrive earlier than 'needed' (in the sense of having enough time to raise young under optimal conditions). This occurs because competition for territories among same-sex conspecifics is a zero-sum game, meaning that one individual's win (gaining a territory) implies another's loss (not gaining it). Investing in succeeding in zero-sum competition has an intriguing property: just like male–male competition over harem ownership does not lead to more harems owned by the population as a whole when males evolve to be more competitive (but male traits can evolve to be costly), outcompeting others in a territorial context does not change the number of territories available but can lead to populations evolving to experience costs related to early arrival. It is therefore entirely possible that the ancestral historical state (before climate change) involves mismatch: individuals arrive earlier than what would be best for population performance. The degree of such a mismatch can initially become reduced if the climate changes and the population has not yet adapted to advance its arrival time to, once again, 'unnecessarily' early times. Later adaptation can restore the mismatch, leading to a corresponding population decline (Johansson and Jonzén 2012b).

This finding has led Johansson and Jonzén (2012b) to state that we might need to consider more complicated causal routes than simple variation in the magnitude of mismatch to explain the observed pattern that declining migratory species tend to be those that have failed to match their phenologies with the changed climate (Tryjanowski et al. 2005, Møller et al. 2008, Saino et al. 2011). If adaptive responses are, in some cases, causally responsible for population declines (see also Kokko 2011), the expected patterns can become much more complex (Johansson and Jonzén 2012a).

Here we focus on an intriguing property that arises from the non-zero nature of competition for territories: it has a tendency to relax when populations decline. If mistimed reproduction leads to lower food availability on average during the breeding season, then the population as a whole is likely to experience lower reproductive success. This will translate to population declines (Both et al. 2006), assuming that population size is at least partially determined by breeding output (i.e. declines in output are not fully compensated for by density-dependence at other times of the year). This leads to a perhaps surprising prediction: the very conditions where climate change necessitates adaptation – population-wide arrival time is now too late, compromising breeding success because of phenological mismatch – selection to arrive early can become less intense than it was before climate change.

The model

Our model considers two distinct selective pressures to arrive early. 1) A bird should leave enough time between arrival and the food peak so that all necessary steps of mate attraction, nest building, laying and incubation can be completed before the food peaks. 2) Fitness also improves with territory quality, and beating other birds in arrival rank is therefore advantageous, as we assume that territories are filled from best to worst, and latecomers cannot usurp territories. Prior to climate change, process 2) can advance arrival times to create a temporal 'safety margin' where no bird experiences strong current selection based on process 1); indeed, arriving for the sole purpose of territory acquisition can occur so early that birds do not need to commence breeding immediately upon arriving. Once the climate changes, the first source of selection 1) is directly impacted, if the food peak advances in time. The second source of selection 2) reflects a zero-sum game. It can be indirectly impacted by climate change via changes in population size: competition eases if the number of competitors is reduced.

Our aim is to make a conceptual point regarding potentially weaker selection to arrive early when processes 1) and 2) interact. For a model to produce evolutionarily stable arrival times, we need, in principle, a third process that counteracts these tendencies by favouring later-arriving individuals. Earlier models have assumed reduced mortality of late arriving individuals (Kokko 1999), or suboptimal subsequent breeding success of too early arriving birds (Johansson and Jonzén 2012a); there is empirical support for both assumptions (Brown and Brown 2000, Bêty et al. 2004). Here we leave these processes outside the model, as our aim is to focus specifically on the strength of selection for advancing arrival. We simply note that regardless of the mechanism producing the third process (or processes) that favours delays in arrival time, its effect will have to be contrasted with the direct as well as indirect effects of climate change on selection to arrive early (processes 1 and 2). If this component of selection weakens while the counteracting selection for a delay remains unchanged, the net effect is selection for later arrival. If selection for a delay is also impacted by climate change, e.g. weakened because early arriving individuals no longer face very adverse environmental conditions, the net effect is that selection on arrival time as a whole weakens.

We assume that the arrival time strategy, T, translates into actual arrival times t as $t \sim N(T, \sigma^2)$, i.e. arrival time in the population is normally distributed with mean T and standard deviation σ. The deviations from T can arise e.g. due to vagaries of weather.

Process 1. Fitness remains intact only if the food peak is not missed

We assume that there is a span of time during which any arrival time leads to best possible use of a territory's resources, because the bird has arrived on time to utilise its breeding territory during the food peak at a suitable point in the breeding cycle. In other words, if a bird arrives early enough before the food peak, it is assumed to be able to arrange its reproductive scheduling to raise a brood optimally (note that our arrival time model does not explicitly model selection on breeding time; Price et al. 1988). But if a bird arrives late, it can only gain a fraction of the reproductive success it would have gained in this territory if food were not a consideration. There is an arrival time, denoted T_0, which is so late that it leads to zero reproductive success. The fraction of success that remains intact, denoted $x(t)$, depends in our example (Fig. 1a) on a bird's arrival time t as

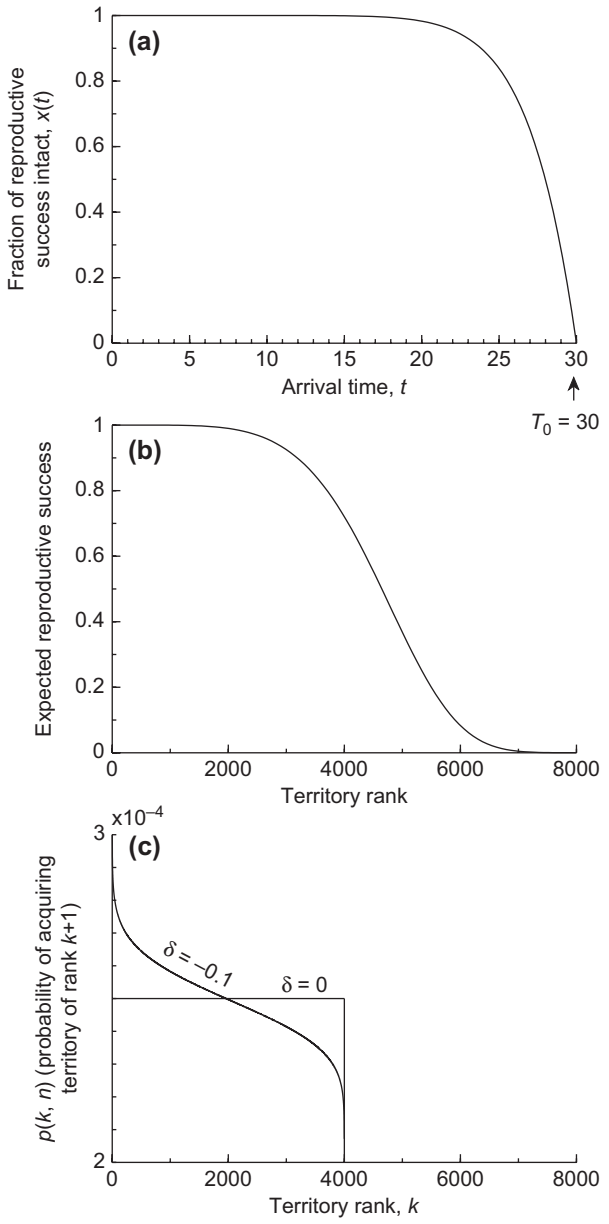

Figure 1. Model assumptions. (a), a graphical representation of Eq. 1 with $\alpha = 10$, which assumes that if a bird has arrived early enough before T_0, it retains 100% (i.e. $x(t) = 1$) of the potential reproductive success offered by its territory. The closer to T_0 the bird arrives, the greater the extent to which its success is compromised ($x(t) < 1$), and arrival time $t = T_0$ or later leads to zero reproductive success. (b), a graphical representation of the relationship between territory rank and its quality (Eq. 3) with $\beta = 5$, $K = 5000$. (c), the probability $p(k, n)$ of acquiring a rank k territory exemplified for a population of size $n = 4000$, for an early arriving mutant ($\delta = -0.1$) as well as an individual whose arrival time is distributed identically to the rest of the population ($\delta = 0$). The latter has an equal probability of acquiring any of the territories $k = 1, 2, ..., 4000$, whereas for the former, there is an enhanced probability of reaching the best territories.

$$x(t) = \begin{cases} 1 - \left(\dfrac{t}{T_0}\right)^{\alpha} & \text{if } t < T_0 \\ 0 & \text{otherwise} \end{cases} \qquad (1)$$

Here α is a parameter that dictates for how close to T_0 the arrival date can be without an appreciable decline in breeding success. Note that this component of selection to arrive early is not zero-sum. If all individuals evolve to advance their arrival time to avoid compromised breeding success because of a phenological mismatch, then population performance is improved as a whole.

Process 2. Zero-sum competition for territories

We assume that territories differ in quality, and early arriving birds obtain better territories. Our argument does not depend on the precise shape of the distribution of territory qualities, nor on the arbitrary assumption, used in our examples, that the best territories will yield breeding success of approximately 1 (Fig. 1b). The numerical example portrayed in Fig. 1b is simply designed to give a good intuitive reason why selection can weaken when a population is reduced in size: if there are, say, 6000 birds, a significant fraction of them will acquire territories in which they cannot raise as many young as in the best territories. By contrast, if there are only, say, 2000 birds, there is barely any difference between the breeding success of birds residing in the best (rank 1) and the worst (rank 2000) territories. This makes it explicit that the strength of selection to arrive early depends on population size.

Selection for early arrival: combining processes 1 and 2

To document the strength of selection for early arrival, the quantity of interest is $S = -[\partial R(T, n)/\partial T]/\bar{R}(T, n)$: here, the component $\partial R(T, n)/\partial T$ describes the change in reproductive success if arriving earlier or later than T, and the minus sign imposes a convention that positive selection refers to earlier arrival being advantageous. The division by $\bar{R}(T, n)$ standardizes the calculation as we may have to contrast results across scenarios where populations differ in their average reproductive output.

We derive the values for S numerically by approximating $\partial R(T, n)/\partial T$ as $(R(T + \delta, n) - \bar{R}(T, n))/\delta$, where δ is a change in the arrival time, $R(T + \delta, n)$ is the expected reproductive success of a mutant who uses arrival time $T + \delta$ instead of T, and $\bar{R}(T, n)$ is the expected reproductive success of an average member of the population using T (see below for its calculation). Thus, for example, if the population-wide reproductive success averages as 0.8 while it is 0.9 for mutant arriving one unit of time earlier (i.e. $\delta = -1$), then $\partial R(T, n)/\partial T$ is evaluated as 0.1, and we compute $S = 0.1/0.8 = 0.125$. Advancing arrival by one unit of time thus leads to 12.5% higher fitness. In practice, we used a smaller value of $\delta = -0.1$, leading to the same computational principles but the quantification of selection then assumes only slight changes in arrival time distributions. This is to avoid artifical effects of mutations of large effect, e.g. a single mutant might be able to outcompete almost all current population members if its timing was dramatically different.

Note that the mutant is also assumed to experience variations in weather conditions, so its actual arrival time is distributed as $\sim N(T + \delta)$. Denote by $p(k, n)$ the probability

that, in a population of size n, exactly k competitors have already arrived at the time when the mutant arrives. The associated arrival time is $t(k)$ (see below why in a large population we can assume a unique $t(k)$ associated with k). The mutant's reproductive success is then

$$R(T+\delta, n)=\sum_{k=0}^{n-1} p(k, n)\, x(t(k)+\delta)\, r(k+1) \quad (2)$$

where $r(i)$ denotes the quality of a territory of rank i (quality equals the expected reproductive success provided in the territory if the bird also exploits the food peak maximally). Note that if $\delta = 0$, the procedure gives the reproductive success of the resident strategy, which we denote by $\bar{R}(T, n)$.

We will derive our examples using a function where the expected reproductive success $r(i)$ (assuming the food peak is not missed) of the ith territory is

$$r(i) = e^{-\left(\frac{i}{K}\right)^{\beta}} \quad (3)$$

where β is a parameter describing how steeply $r(i)$ declines with territory rank, and K scales the overall number of territories (these two determine equilibrium population sizes as we will detail below).

If we assume that the population is not very small, we can derive $p(k, n)$ using the following approach. We first derive $P(k, n)$ as the probability of having maximally (rather than precisely) k competitors arriving before the focal mutant, from which we then get $p(k, n) = P(k, n) - P(k-1, n)$ if $k > 1$ and the special case $p(1, n) = P(1, n)$. Finding $P(k, n)$ is based on knowing that the mutant has an arrival time distribution $N(T + \delta, \sigma^2)$ while other population members are distributed as $N(T, \sigma^2)$. Denote by $t(k)$ the time point at which the cumulative distribution of $N(T, \sigma^2)$ reaches the value k/n (this is found numerically by solving $k/n = 1/2\,(1 + \mathrm{erf}(t(k) - T/\sqrt{2\sigma^2}))$ for $t(k)$, where erf() denotes the mathematical entity known as the error function). This indicates that k out of the n resident population members have arrived by time $t(k)$. Therefore, if the mutant arrives by $t(k)$, it will have maximally k competitors ahead of it. The probability that the mutant does so is equal to the cumulative distribution of $N(T + \delta, \sigma^2)$ at $t(k)$, thus we have $P(k, n) = 1/2\,(1 + \mathrm{erf}(t(k) - (T+\delta)/\sqrt{2\sigma^2}))$. The sequence of $P(k, n)$ values then gives the $p(k, n)$ sequence as indicated above.

The general outcome is that $\delta < 0$ leads to enhanced probabilities of acquiring good territories, while $\delta = 0$ leads to a uniform distribution of rank acquisition prospects among the best n territories (Fig. 1c). Equation 3 then weights the expected reproductive success from each territory with the probability of reaching that territory.

Note, however, that our procedure is necessarily approximate: at very small population sizes the stochasticity in arrival time distributions and the fact that the mutant's presence reduces the number of 'other' competitors would render our approximation potentially suspect to error (i.e., not exactly half of competitors will in all realizations of the process have arrived by time T, and thus there is not a unique time point $t(k)$ associated with a certain rank, but a distribution). The method performs adequately when the populations are not very small; our examples assume thousands of individuals for this reason. Note that there are also other reasons, e.g. drift, why selection can become ineffective if populations are very small (Lanfear et al. 2014).

Population dynamics: how many competitors will there be?

To maintain generality, we will not specify all assumptions for a full life cycle. Instead, we simply assume that a certain level of productivity, denoted R_{thres}, must be maintained by the population for it to be stable. In the example of Fig. 2, we show the consequences of an assumption that year-round mortalities of adults and juveniles must be compensated for by breeding success of at least $R_{\mathrm{thres}} = 0.75$ per territory for the population to grow; less than 0.75 leads to a decline. One possible way that an annual cycle can lead to this situation is that 70% of adults and 40% of juveniles survive: $1 \times 0.7 + \bar{R}(T, n) \times 0.4 = 1$ when $\bar{R}(T, n) = 0.75$, thus the population is stable.

The requirement of a certain average productivity creates density dependence (Fig. 2): larger populations will be less productive per capita (i.e. have a smaller $\bar{R}(T, n)$), as an increasing proportion of birds breed in poor quality territories. Because populations that miss the resource peak are assumed less productive, the curves that link the breeding population size n to its *per capita* productivity (Fig. 2) also depend on T, the average arrival time used by the population. If T is close to T_0, the temporal 'safety margin' between actual arrival and the time point that is too late for raising of young is very short, and reproduction will then often fail even in the best territories (in Fig. 2, the two lower curves show T that is only 5 or 10 time units away from T_0).

Using our example of $R_{\mathrm{thres}} = 0.75$ as the required breeding success for stability, the breeding populations will

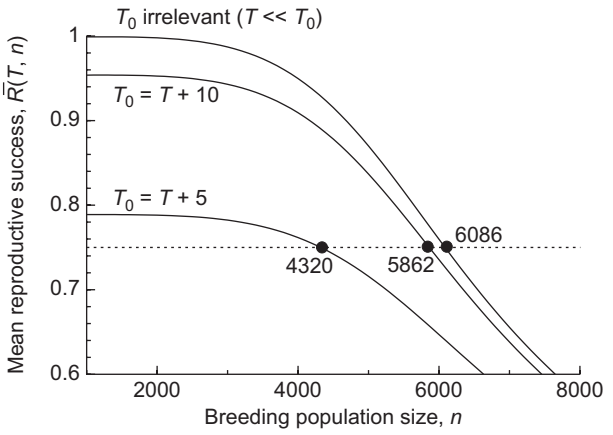

Figure 2. The population dynamic consequences of the assumptions (Fig. 1): mean reproductive success $\bar{R}(T, n)$ declines with population size n, and it also declines when birds arrive not far ahead of T_0 (this temporal distance is large for the uppermost curve, smaller for the middle curve, and smaller still for the lowest curve). If we assume that per capita reproductive success of at least 0.75 is required to avoid population decline, the population will stabilize at 6086, 5862 and 4320 breeders, respectively. Alternative assumptions can also be read from the same graph (e.g. a requirement of 0.8 would lead to smaller population sizes and/or to extinction, as no territory has productivity 0.8 in the example where $T_0 = T + 5$). Parameter values: $\sigma = 2$, $\alpha = 10$, $\beta = 5$, $K = 5000$.

consist of 6086 birds if birds arrive well ahead of T_0 such that no bird has reduced reproductive success because of having missed the peak ($T << T_0$). The population, however, declines to 5862 birds if birds arrive on average only 10 time units before T_0, and to 4320 birds if they arrive, on average, 5 units before T_0. Obviously, a short safety margin between T and T_0 can come about in two ways: the population can evolve to be close to T_0, or T_0 can shift because of climate change.

What does it mean for the population?

All else being equal, reducing the safety margin, i.e. the time interval between the time where it is too late to arrive (as the food peak will be missed), T_0, and the current average arrival date, T, leads to stronger selection to arrive early (Fig. 3). As stated above, one way in which the safety margin can become shorter is climate change (arrow in Fig. 3). For example, selection to arrive early intensifies by approximately 25% if $T_0 - T$ shifts first from a large value (e.g. 30 time units) to 10, and then to only 5 time units (arrow with open symbols in Fig. 3).

However, the statement 'all else being equal' proves important: importantly, it assumes that the population has not declined. If this remains true, then we can follow the same curve in Fig. 3 throughout climate change, as in the above example. Consider, however, that the resource peak advance has another effect on the population: before any evolutionary change has taken place, it causes the population to decline. Mean breeding success is reduced because fewer birds are able to breed in time before the food peak is finished. Figure 2 predicts a decline from 6086 birds to 5862 birds when $T_0 - T$ is reduced from a large value to 10 time units. If this happens, then selection to arrive early becomes somewhat weaker. It becomes weaker still, if the population declines further as $T_0 - T$ is reduced to 5 time units (Fig. 3, arrow with filled symbols).

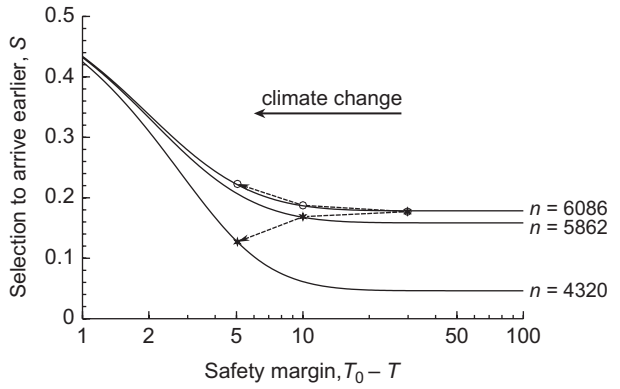

Figure 3. The immediate effect of climate change in the model is to shift resource availability to earlier dates, which reduces the 'safety margin' of bird arrival dates, i.e. the distance between T_0 and T. If populations were of constant size, selection S would always intensify when $T_0 - T$ is reduced (the direct effect of climate change). However, given that populations are expected to decline, the net change must combine this indirect effect (relaxed selection in lower curves compared with the upper ones) with the direct effect. The net effect may then be relaxed selection to arrive early when T_0 shifts to earlier dates. Parameter values as in Fig. 3.

Generality

Is the result of Fig. 3 general? We investigated this question by creating 250 sets of parameter values where we varied σ, α, β, K and R_{thres} in a manner specified in Table 1. We picked (randomly, independently and without replacement) one value for each of the parameters from this table and computed the data equivalent to that of Fig. 2, until we had 250 replicates featuring all three population equilibria (Fig. 2) being at least 1000 individuals strong. Collecting 250 such cases required 276 parameter sets, thus approximately 9% of parameter choices in Table 1 lead to such small populations that we do not necessarily trust our method to approximate evolution well enough (while we discarded these cases, they did not contradict our key findings.

We then asked whether these 250 cases differ qualitatively from the key finding of Fig. 3. This key finding can be expressed numerically as two criteria: 1) the value of S at the upper arrow's tip should be higher than the value of S at the root of this arrow (in other words, if population sizes did not change, climate change would intensify selection for early arrival); 2] the value of S at the lower arrow's tip should be lower than the value of S at the root of this arrow (in other words, given that population sizes will change, selection can weaken). At least for Fig. 3's choices of $T_0 - T$, both criteria were always true for all 250 cases we examined; they also remained true in every case if we included cases where population sizes were potentially too small for our method's trustworthiness. Interestingly, the difference in S was typically smaller in 1) (focusing on the valid 250 cases: mean difference between tip and root of arrow = 0.061, range 0.0096...0.15) than in 2) (mean 0.93, range 0.060...4.9), which replicates the pattern we found in Fig. 3: the reduction in the intensity of selection, caused by population declines, is stronger than its potential intensification in a population of constant size.

Discussion

Population declines reduce the strength of competition between birds for high quality territories (Kokko 1999). Although intuition suggests that birds should advance their arrival time to track the food peak, our results add to a

Table 1. Parameter values in figures, and the set of values that forms the basis of our generality argument. Note that we chose a logarithmically scaled set of values for σ, to reflect our prior assessment that small changes in the variance might have a more important effect when σ is small, thus we test for more values between 0.1 and 0.11 than between 9.99 and 10.

Name	Value in figures	Values created for random runs
α	10	1000 linearly spaced values between 2 and 20 (i.e. 2, 2.018, 2.036, ..., 20)
β	5	1000 linearly spaced values between 2 and 10
K	5000	1000 linearly spaced values between 3000 and 8000
R_{thres}	0.75	1000 linearly spaced values between 0.5 and 0.9
σ	2	1000 logarithmically spaced values between 10^{-1} and 10 (i.e. log(σ) is linearly spaced with values –1, –0.998, ..., 1)

growing body of knowledge of various reasons (Visser et al. 2004, Visser and Both 2005, Jonzén et al. 2007, Saino et al. 2011) why this might not happen perfectly or, in some cases, at all. If a phenological mismatch causes the population to decline before it has had time to respond evolutionarily to the new situation, the evolutionary response might never happen. Stronger selection to arrive early, due to the novel mismatch, can be counteracted by reduced selection to arrive early caused by the population decline. This indirect effect of climate change can be stronger than the direct process.

Note that we left all processes outside our model that select for later arrival. Thus, selection is always positive in our model (meaning, by our convention, selection for earlier arrival) but varying in strength. The effect of any process that counteracts the push towards earlier arrivals is nevertheless easy to visualize. If the population was initially at equilibrium despite our positive selection gradient, then in the new situation (where the positive gradient has become weaker) it is possible that populations experience net selection to arrive later. This, obviously, would further intensify the phenological mismatch, and lead to further population declines, at which point territorial competition is even more relaxed. Together with the expectation that the strength of natural selection can become swamped by drift in small populations (Lanfear et al. 2014), our model raises the possibility of a vicious circle where an evolutionary rescue, a process that restores the capacity of a population to grow in novel environmental conditions (Bell 2013), becomes very unlikely.

Our model, obviously, has limitations. Most importantly, its take on population dynamics is simplistic: we do not assume that a smaller number of breeders elevates the breeding success of the remaining breeders in any other way than by an 'ideal despotic' process (Fretwell 1972) where territories are filled in strict rank order of declining quality, and birds have perfect information on these qualities. Neither have we modelled any compensatory density-dependence in mortality rates, which might mitigate the effects of reduced breeding success due to climate change. At one extreme, it might be the case that reduced breeding success does not alter the number of birds competing for breeding positions in the spring. Such an alternative may be considered unlikely, as there is much evidence for density dependence of birds operating via pre-emptive use of territories ('ideal despotic distribution', Ferrer and Donazar 1996, Petit and Petit 1996, Krüger and Lindström 2001, Rendón et al. 2001, Zimmerman et al. 2003, Sergio et al. 2007). Nevertheless, any degree of compensatory mortality operating in the non-breeding season would make our findings less severe.

The set of model assumptions also include other simplifications that further work could usefully relax. We assumed that all birds are of equal quality, while in reality, selection might be weak if only low-quality latecomers miss the resource peak. On the other hand, the population dynamic consequences might in those cases be simultaneously less severe. We assume no 'waves' of birds arriving based on e.g. weather patterns or the circadian rhythm that dictates migratory activity by time of day, and we do not model the search for territories (or prior knowledge based on past ownership) explicitly.

Perhaps more importantly still, we have also left the roles of two sexes unspecified in our model. In reality, the benefits of early arrival are not only associated with an increase in territory quality, but there could also be processes acting on mate acquisition, such as enhanced breeding success because a shorter time is required to find a mate and start breeding (Møller 1994, Currie et al. 2000), obtaining a better-quality mate (Arvidsson and Neergaard 1991, Lozano et al. 1996, Huyvaert et al. 2006) and increased extra-pair success (Langefors et al. 1998, Huyvaert et al. 2006). The differing roles of male and female arrival times as determinants of population dynamics have attracted little theoretical attention, despite empirical work showing its importance both for evolution (Spottiswoode et al. 2006) and ecology (Smith and Moore 2005). In this context it appears intuitive to predict that early male arrival does not help much if females are not arriving early enough to commence breeding in time. It may therefore be best to view our model as zero-sum competition between females; further work on two-sex arrival timing models appears desirable.

Despite our model's limitations, our results are conceptually interesting as they extend beyond implications for how migrating birds in the wild might respond to climate change. Much of theory (Gomulkiewicz and Houle 2009, Chevin and Lande 2009, Kirkpatrick and Peischl 2013) as well as experimentation (Bell and Gonzalez 2009, Cameron et al. 2013) on evolutionary rescue has used abiotic challenges as examples (but see also Bonte et al. 2009). In such cases, selection typically works on traits that benefit populations in a manner that is not zero-sum: the entire population can grow better if individuals perform well. However, our examples show that phenology combines zero-sum and non-zero sum processes, and this can substantially complicate predictions and make them as a whole more pessimistic. The only parameter region where we would not predict relaxed selection is a case where the temporal 'safety margin' (denoted $T_0 - T$ by us, Fig. 3) is already very small. In these cases selection to arrive early remains intense, but simultaneously reproductive success is predicted to be very low, and the future of such populations is demographically uncertain.

It is also of interest to note that our results can switch the direction of causality in the interpretation of across-species comparisons, where greater mismatches associate with greater population declines (Tryjanowski et al. 2005, Møller et al. 2008, Saino et al. 2011). It remains possible that a large mismatch causes a large decline, and no other process is needed to explain the pattern. However, our results suggests an additional possibility: an initial decline is the cause for a failure of a population to respond evolutionarily to the mismatch. If the process outlined in our model is operating, the two directions of causality can become a feedback that prevents, rather than promotes, adaptation.

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